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## A STUDY OF SOMATIC CHROMOSOMES.

### I. THE SOMATIC CHROMOSOMES IN COMPARISON WITH THE CHROMOSOMES IN THE GERM CELLS OF *Anasa tristis*.

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With the exception of incidental and scattered observations in connection with studies on spermatogenesis there have been only a few papers of a statistical nature on the number, type and combination of the chromosomes in somatic tissues. Usually, and more or less arbitrarily, the diploid or gonial number of chromosomes of the germ cells has been assigned to the cells of the soma. However, the number of chromosomes in the somatic cells is not necessarily the same as that in the germ cells. Cases have been reported, for instance, in *Ascaris*, some of the Hymenoptera, a Lepidopteran, and in several of the Vertebrata, where the somatic number of chromosomes is higher than the gonial number. On the other hand in *Culex*, *Diaptomus*, *Phascolosoma*, and some of the Diptera the number of chromosomes may be lower in some or in all of the cells of the body tissues than in the gonidia.

Extensive studies on the development of the germ cells in animals have, in general, offered strong evidence for an "individuality" of the chromosomes. Variations in the number of chromosomes in the germ cells are relatively infrequent. This undoubtedly is of the greatest importance in the modern "chromosome theory" of heredity. At first hand the peculiar history of the chromosomes in somatic cells of certain animals may seem to render somewhat untenable this theory of the "individuality" of the chromosomes, and may easily give rise to the idea that they are exceedingly variable structures. With this in mind, a study is being made of the chromosomes in the somatic tissues of various developing embryos for the purpose of determining if chromosomes of the somatic cells generally agree in number and

type with those of the germ cells. Apparently any peculiar history of the chromosomes in somatic cells must be regarded as a concomitant of differentiation. This atypical "behavior" of the chromosomes, in lieu of a better explanation, has been satisfactorily accounted for from the standpoint of the doctrine of the "individuality" of the chromosomes in the following manner: in those forms where the chromosomes exist in the somatic cells in greater number than in the germ cells, investigators generally agree that the chromosomes of the sex cells are bivalent or plurivalent. These chromosomes fragment probably quite early in the development of the embryo, as has been shown in the case of *Ascaris* and that of the Hymenoptera. Conversely, where the number of the somatic chromosomes is lower than the number of the chromosomes in the sex cells, there is a more or less permanent pairing or fusion of the chromosomes in the soma.

Accordingly the behavior of the chromosomes in the soma can be tentatively summarized in the following manner:

1. All of the chromosomes in the gametes are univalent, and are of the same number and type in all the cells of the body, both somatic and germinal.

2. The chromosomes of either one or both of the gametes are compound, and in one of the early cleavages of the egg fragment into their component parts in the cells giving rise to the soma. This procedure clearly distinguishes the *Keimbahn* from the soma by establishing a dissimilarity between the two in the number and type of their chromosomes.

3. The production of double or multiple chromosome groups by the suppression of cell division.

4. All of the chromosomes of both gametes are univalent, but become bivalent in the cells of the soma by a more or less permanent fusion with other chromosomes. The resulting chromosomes appear univalent.

A consideration of this problem will tend to strengthen the view that the chromosomes, to a certain degree at least, are constant and not variable structures, and that they possess a certain morphological identity in the majority of animals. In the case of *Anasa*, with which this paper deals, there are certain

definite size relations among the chromosomes in the germ cells, and these size relations can be followed out successfully in the various tissues of the body.

This series of investigations was taken up at the suggestion of Prof. E. G. Conklin, and I wish to express my gratitude to him for his interest in and helpful criticism of these investigations. I am also indebted to him for the use of his slides on the spermatogenesis of *Anasa*.

#### MATERIAL AND METHODS.

The eggs of *Anasa tristis* in various stages of development were obtained in abundance on the leaves of squash plants during the months of July and August. The method of fixation, which gave the best results, was that of Carnoy and Lebrun. This fluid consists of equal parts of absolute alcohol, chloroform, and glacial acetic acid, with the addition of mercuric chloride to saturation. Eggs were well fixed in this fluid in from fifteen to twenty minutes. From this fluid the eggs were transferred to iodized 95 per cent. alcohol for twelve to eighteen hours, and were then preserved in 80 per cent. alcohol. The eggs are surrounded by an extremely tough chorion which must be removed before sectioning.

Larval ovaries were fixed for several hours in Flemming's strong solution. This same solution was also used in making preparations of the testes.

Sections of both the sex glands and the eggs were cut 7-10 micra in thickness. Owing to the presence of the yolk in the eggs, which becomes somewhat brittle after fixation, it is often of advantage to separate the embryo from the yolk before embedding, though this tendency of the yolk to crumble may be obviated to a certain degree by the addition of a small amount of crude rubber to the stock solution of paraffin.

The stain employed in all cases was Heidenhain's iron-hæmatoxylin, with or without a counter-stain of erythrosin. The value of a counter-stain is extremely doubtful, and perhaps the best preparations were obtained by a long immersion in the hæmatoxylin, which stains the chromosomes black but leaves the cytoplasm a light gray or almost colorless after destaining.

All the figures were drawn at table level with the aid of an Abbé camera lucida, using a Leitz 18 compensating ocular and a 2 mm. apochromatic objective, and are reproduced here at a reduction of one third. In a few cases it was necessary for the sake of clearness in the reproductions to draw one or two chromosomes out of their true positions. The chromosomes linearly arranged were drawn from the actual specimens, and not traced from the drawings of the plates.

Mitotic figures occur throughout the embryos and are numerous, but it must not be supposed that the chromosomes in many of these figures can be counted. It is sometimes necessary to section twenty-five or more embryos before finding a division figure which is clear. In this connection the remarks of Metz ('16, p. 215) are pertinent: "Although certain principles must be observed in making preparations, the task is mainly one of securing and preparing enough specimens to get material in the proper stages and in sufficient quantity for study."

#### OBSERVATIONS.

*Anasa tristis* is an exceedingly favorable form for this particular problem, since the chromosome complex is so well known, and since it has been described by several investigators with general unanimity in result. The striking size differences of the chromosomes of one plate also makes it an excellent form for study.

In order to understand the nature and character of the chromosome complex, it will be necessary to review briefly the description of the spermatogenesis and oögenesis of this species. Wilson ('05b) ('06) showed that the number of chromosomes appearing in the spermatogonial divisions was 21. Three of these chromosomes are larger, and two are very much smaller, than the others, so that there is a marked differentiation in size in any one group. Of these 21 chromosomes, 20 can be paired, leaving one the largest, unpaired. This largest chromosome is the *x*-chromosome (accessory). The two smallest have been termed the *m*-chromosomes, and are distinguished by the fact that they do not unite to form a bivalent chromosome in the growth period, but condense as two separate chromosomes, pairing in the first

maturation division, and immediately separating without fusion. The  $x$ -chromosome divides equationally in the first maturation, but in the second division passes undivided to one of the poles of the spindle. In this way a dimorphism of the spermatids is established, and later, a dimorphism of the spermatozoa, with respect to their chromatin content, one half containing 10, and the other half 11 chromosomes.

The oögonia on the other hand contain 22 chromosomes, four larger than the others, and two very small  $m$ -chromosomes. In the metaphase of the first oöcyte division (Morrill, '10) there are eleven chromosomes, many of them appearing as tetrads. Two of the chromosomes are larger than the others, the  $m$ -chromosomes are fused and appear as a single tetrad, and all of the chromosomes divide equally. In the metaphase of the second maturation division there are 11 dyads, two larger and one (the  $m$ -chromosome) smaller than the others.

To express, then, the possible combinations of the chromosomes at fertilization, we have the following formulæ, letting  $x$  stand for the  $x$ -chromosome,  $M$  for the macrochromosomes (the large chromosomes), *meso* for the mesochromosomes<sup>1</sup> (those intermediate in size), and  $m$  for the  $m$ -chromosome:

1. ♂ gamete ( $x + M + 8 \text{ meso} + m$ ) + ♀ gamete ( $x + M + 8 \text{ meso} + m$ ) = ♀ embryo ( $2x + 2M + 16 \text{ meso} + 2m$ ).

2. ♂ gamete ( $M + 8 \text{ meso} + m$ ) + ♀ gamete ( $x + M + 8 \text{ meso} + m$ ) = ♂ embryo ( $x + 2M + 16 \text{ meso} + 2m$ ).

The results summarized in these two equations were determined by Wilson and Morrill, and are confirmed by my investigations.

Wilson ('06) figures a group of chromosomes from a dividing follicle cell of the ovary. There are 22 chromosomes, corresponding in their size relations to the anticipated result mentioned above. Although he gives no figures, he states that the cells in the ectoderm of the larvæ contain approximately the same number of chromosomes as do the oögonia. He also figures a plate from a cell toward the periphery of a larval ovary in which

<sup>1</sup> It has become necessary to find some word by which chromosomes not characterized by their size or behavior can be designated. The term "autosome" is too comprehensive. Accordingly I have used the term *mesochromosome*, the prefix being derived from the Greek adjective μέσος meaning *intermediate in size*.

there are 44 chromosomes. This includes eight macro- and four *m*-chromosomes. He concludes, therefore, that a division of the chromosomes had taken place without a subsequent division of the cell body, and further states that such a condition is not uncommon in the investing cells of the ovary, of the oviduct, and of the fat body. These cells are considered by him as either degenerating or as highly specialized.

Morrill ('10) figures "incomplete blastoderm" mitoses in the developing eggs of *Anasa*, and finds that there are two kinds of embryos with respect to their chromosome content, one containing 21, and the other 22 chromosomes. The two different chromosome groups correspond, respectively, to the groups found in the spermatogonia and the oögonia, showing the same size differences and the same number of the various types of chromosomes. He also reports one case of 23 chromosomes, but suggests that this is due to an accident in technique.

The results presented in the present paper were obtained from several stages in the developmental history of *Anasa*. These stages can be grouped, roughly, under three heads: I. Late cleavage (pre-blastodermic) and early blastodermic; II. Appearance of the limb buds, and first indications of segmentation in the embryo; III. Shortening of the elongate embryo. Of these stages, stage I. shows the clearest and most diagrammatic chromosome plates. The second stage shows division figures in the undifferentiated ectoderm, and stage III. was excellent for mitotic figures in neuroblasts, the mesoderm, and the hypodermis.

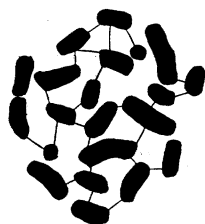
In these stages over 100 counts were made of equatorial or pre-equatorial plates. The difficulties first experienced were stated in a preliminary paper (Hoy, '14), as was also the explanation of some plates apparently containing an atypical number of chromosomes. It must be borne in mind that in some cases there appears to be a diversity in the chromosome number of different cells, but in all these plates the chromosomes are crowded together making an enumeration extremely difficult. However, there seems to be no case where an explanation of an apparently aberrant number cannot be made, logically and clearly, on the grounds of accidents in technique, overlapping of the chromosomes, or apparent fusion of several chromosomes due to poor

destaining. Foot and Strobell ('13, p. 199) have particularly objected to such explanations, characterizing them as "the old story so familiar to cytologists—if a feature is where, hypothetically, it ought not to be, it is an artifact, and if it is not where it ought to be, it is due to faulty technique." Their objections are valid, I think, up to a certain point. Variations may easily occur, in fact the double chromosome groups in *Anasa* are proof that they may occur frequently. As to the total disappearance of chromosomes I have no proof. Moreover, the metaphase plates which have been studied are all reasonably clear and no variations in the number or type of the chromosomes have been demonstrated, other than the above. It seems reasonable, therefore, not to entirely ignore the above-mentioned explanations, especially since the preponderance of proof is in favor of the characteristic chromosome number. If an entire chromosome plate lies in one section, and is sufficiently clear to be counted, the normal number has invariably been found (with the exception noted). It is well to point out that the study of prophases has been found to be unadvisable owing chiefly to the inaccuracy of the enumerations, due to the overlapping of the chromosomes.

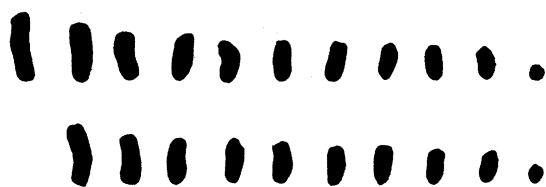
Figs. 1-4 show plates of the 21-chromosome type. To the left are the chromosomes as they appear in the plates, and to the right the chromosomes linearly arranged. Fig. 1 is a spermatogonial metaphase. Fig. 2 a late cleavage metaphase, Fig. 3 is from a neuroblast in division, and Fig. 4 from an abdominal mesoderm cell. The last two figures are from the same embryo at a stage of development corresponding to stage II.

Bearing in mind the 21-chromosome complex previously mentioned, it will be seen that in all these figures there are 2 *m*-chromosomes and 3 chromosomes larger than the others. One of these three larger chromosomes, the largest, is obviously unpaired. In the eight pairs of mesochromosomes there is a gradual gradation in size from the macrochromosomes to the *m*-chromosomes. Aside from this decrease in size they show no striking peculiarities. The attempt to arrange the chromosomes in pairs is, of course, an arbitrary one, but it will readily be seen that, with the exception of the unpaired largest, there are two

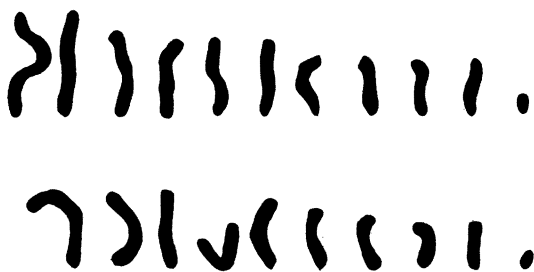




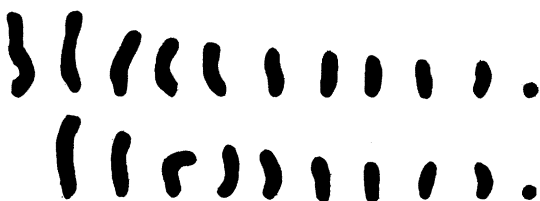
1



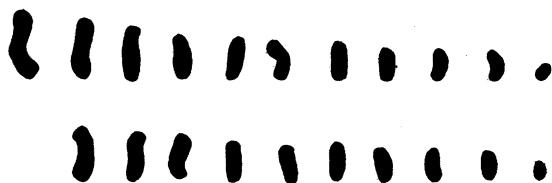
2



3



4



*Anasa tristis*. 21 chromosomes, male type. Fig. 1. Spermatogonium. Fig. 2. Cleavage nucleus. Fig. 3. Neuroblast. Fig. 4. Mesoderm.

chromosomes of approximately the same size at each step in the gradation.

The spermatogonial chromosomes are short and thick, and the

closest resemblance to these is shown by the chromosomes of the mesoderm cell (Fig. 4). However, in both of these cases the cytoplasmic areas of the cells are much smaller than those of the cells in which the more elongate chromosomes of Figs. 2 and 3 appear. This much elongated appearance of the chromosomes is characteristic of both neuroblasts and late cleavage cells, the nuclei and cytoplasmic areas of which are larger than those of the other cells. One must also take into account the fact that the apparent size and volume of the chromosomes is influenced to some extent by the length of extraction of the stain. Realizing this, the figures produced in this paper have been taken from preparations as far as possible stained alike.

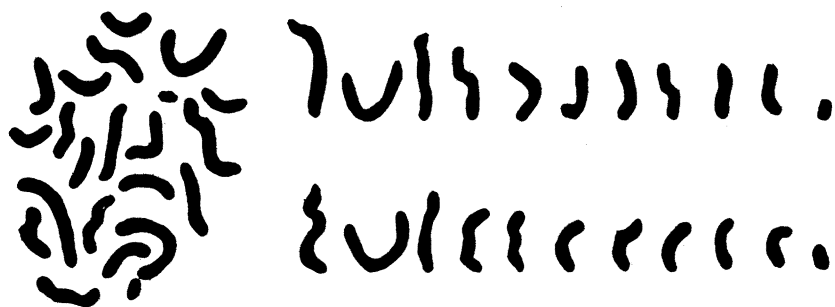
Figs. 5-8 are from embryos showing the 22-chromosome type. Here again the formula of the 22-chromosome complex, previously outlined, is confirmed. There are four macrochromosomes in each figure, the difference, as contrasted with the 21-chromosome type, being that the largest chromosome is found paired. Fig. 5 is from a late cleavage cell and, as was the case in corresponding plates of the 21-chromosome type, the chromosomes are much elongate. Fig. 6, from a neuroblast in the cerebral ganglion, was drawn from the finest preparation obtained in all the series. The chromosomes are not as large as in Fig. 3, but this figure is taken from an embryo of about stage III, while, as was pointed out, Fig. 3 is from an earlier stage.

Figs. 7 and 8 are also from embryos corresponding in their development to stage III. Fig. 8 is from a cell in the hypodermis of the antenna. This cell is of small size, and the chromosomes are the smallest of any group shown.

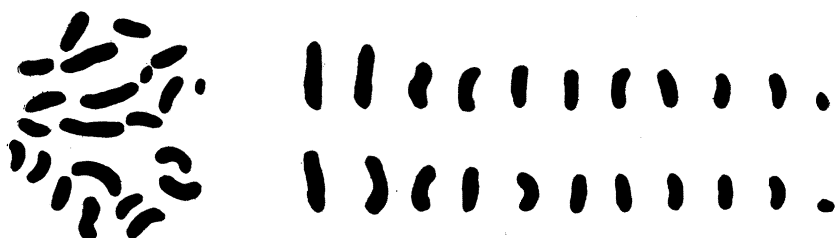
Fig. 9 is from an oögonial mitosis. The 22-chromosome type found in the developing embryos corresponds to this in the same manner as the 21-chromosome type corresponds to the spermatogonial plate. Fig. 10 is from a dividing cell in the oviduct, and furnishes additional proof that the 22-chromosome type is the female type, and is the number characteristic of the somatic tissues as well as the sex glands of the female.

In addition, cases of double chromosome groups were found in connective tissue cells surrounding the young ovary. These groups correspond to Wilson's report of 44 chromosomes in certain investing cells of the ovary. Since the number is double

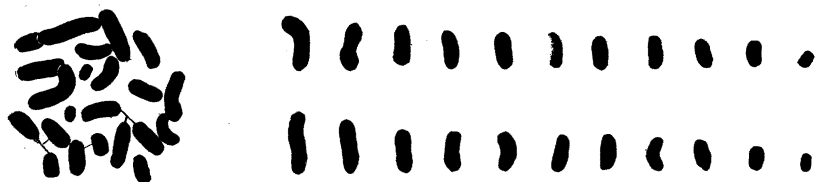
the normal somatic number, and since the chromosome pairs are evidently doubled, it is highly probable that, as he suggests, there was no division of the cell after the division of the chromosomes. Whether these cells are degenerating or are highly specialized is of course problematical, but they do not affect the



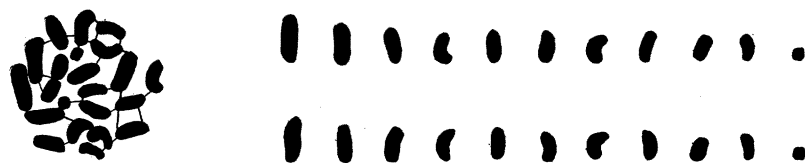
5



6



7



8

*Anasa tristis*. 22 chromosomes, female type. Fig. 5. Cleavage nucleus. Fig.

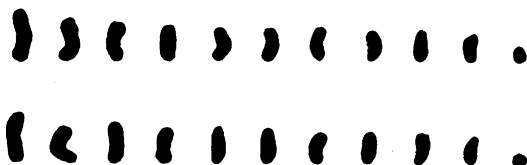
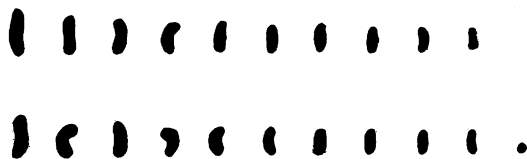
6. Neuroblast. Fig. 7. Mesoderm. Fig. 8. Ectoderm.

view that the normal somatic chromosome number is a constant one in *Anasa*.

It is evident, then, that the embryos of *Anasa tristis* fall into two classes with respect to their chromosome content, one containing 21, and the other 22 chromosomes in all the cells of the various tissues where an examination was possible, with the one exception noted. These conditions are found in every plate



9



10

*Anasa tristis*. 22 chromosomes, female type. Fig. 9. Oögonium. Fig. 10. Epithelium of oviduct.

where it is at all possible to make an accurate count. In some cases the *m*-chromosomes lie so near the largest chromosomes that it is difficult to distinguish them. Even in metaphase groups where a count is impossible, it is possible to identify many of the chromosomes.

Aside from the general constancy in the number of the chromosomes in these embryos, the most important and significant fact is that of the constancy in type. The individuality of the chromosomes is represented by this constancy of type, and it is clear that in *Anasa* this is not confined merely to the chromosomes in the sex cells, but occurs throughout early embryonic development in the somatic tissues, and it is logical to suppose from this that this constancy in type of the chromosomes is present throughout the entire life cycle of this animal. Of similar importance is the fact that definite pairs of chromosomes can be

demonstrated in the various tissues of developing embryos. From a comparison of the diploid groups in spermatogonia and of those in oögonia, together with the haploid groups, which have been described by Wilson and Morrill, it is clearly evident that the members of these pairs of chromosomes are derived one from the male parent and one from the female parent.

Though the same size relations seen in the chromosome complex of the germ cells is reproduced in the somatic cells, there is a difference in size and volume of the homologous pairs in different cells. This difference can probably be explained upon the grounds of a greater or less metabolic activity of the nucleus; that is, difference in size may be due to a real increase in the amount of the chromatin. On the other hand it may be due merely to the swelling of the chromosomes by absorption. Conklin ('12) found that "the chromosomes of the spermatid are usually smaller than those of the oötid, but when the chromosomes of the first cleavage spindle appear, those from the sperm nucleus are usually as large as those from the egg. The reason for this is to be found in the fact that both grow, after fertilization, in the same medium, the egg plasma, and for approximately the same length of time." He found that the size of the chromosomes is dependent upon the size of the nucleus from which it comes, and that in general the small nuclei gave rise to chromosomes smaller in size than those which came from a large nucleus.

So far as has been determined, none of the chromosomes in the somatic cells are distinguished by any peculiar behavior. All the chromosomes seem to divide at about the same time, and in the same manner. The division plane is a longitudinal one, separating the chromosomes into morphological identical halves, as can be demonstrated in polar views of anaphases. In some cases the individuals of a pair lie very close together, but this is an extremely inconstant feature. Beyond a difference in size it is usually impossible to distinguish various chromosomes by any peculiarity of shape, since the same pair may appear U-shaped, slightly curved, or as straight rods in different cells, and one chromosome of a pair may even differ very much in shape from its mate. This is probably due to the position of the particular chromosome in the equatorial plate, and to some difference in tension of the spindle fibers.

## CONCLUSIONS.

1. The somatic number of chromosomes in *Anasa tristis* is constant, with the one exception, namely, that double chromosome groups occur in certain investing cells of the ovary.

2. There are two classes of embryos, one with a complex of 21 chromosomes, the other with a complex of 22 chromosomes in all the cells of the various tissues of the body which have been examined, with the exception noted.

3. The chromosomes in the somatic cells are of the same number and type as those in the germ cells. The 21-chromosome type corresponds to the spermatogonial complex, and the 22-chromosome type to that of the oögonia. Accordingly, embryos having 21 chromosomes in the somatic cells are males, those with 22 chromosomes, females.

4. The male somatic chromosome complex consists of 3 macro-, 16 meso-, and 2 *m*-chromosomes, which is the same as is found in the spermatogonia.

5. The female somatic chromosome complex consists of 4 macro-, 16 meso-, and 2 *m*-chromosomes. This corresponds to the oögonial complex.

6. These facts show that there is both an identity of number and an identity of type in the chromosome complexes. The identity of type is further emphasized by the fact that definite pairs of chromosomes can be demonstrated in these groups.

7. The double chromosome groups do not represent fragmentation or transverse splitting of the chromosomes, for the female formula is doubled and this evidently has been brought about by the failure of the cells in question to divide after a division of the chromosomes had taken place.

## REVIEW OF LITERATURE.

The following table is composed of the counts which have been made of the chromosomes in somatic cells. In a great many cases these counts have been incidental to a study of the sex cells, and have served, in the main, merely to substantiate the counts of the diploid number of chromosomes in the sex cells. It is an unfortunate fact that the term "somatic number" is frequently used for that of "diploid number" of the germ cells. In a few cases it has been impossible to determine whether the

author has actually counted the chromosomes in somatic cells or has really meant the diploid number of chromosomes in the sex cells. Since the two numbers are not alike in many animals, the use of the former term in this connection should be abandoned.

This is not intended to be an exhaustive list of the literature on the subjects of spermatogenesis or oögenesis. Only where accounts do not agree is reference made to more than one author. A number of papers on oögenesis have reported counts of chromosomes in the early cleavage of the egg. For the most part these reports have not been included here, since counts of the chromosomes in the first or second cleavages can hardly be considered as conclusive of the somatic number, except where the *Keimbahn* has been determined and where definite statement is made of the particular cell in which the chromosomes were observed. When the counts made in the early cleavage are followed up by counts in the germ layers or their derivatives they then become of significance. In this connection I have omitted the counts of chromosomes in the early cleavage of Echinoderms, and of the lower worms, in both of which groups numerous counts have been made. Obviously, too, cases where only a few counts have been made in one tissue are not at all conclusive when unaccompanied by counts in other tissues. However, since these are from definite somatic tissues they have been included here.

In the alloiogenetic forms only the sexual generations are included, since the purpose of this table is the comparison of the number of the chromosomes in the sex cells with those in the somatic cells. Investigation has been made on the chromosomes of parthenogenetic individuals in a number of forms, particularly in the Hymenoptera, the Aphididæ, and in the Crustacea. (Morgan, Stevens, etc.)

Where two different numbers are given for the haploid or reduced number, this refers to the fact that an accessory chromosome (or chromosomes) is present, and where the two haploid numbers are the same, to the fact that idiochromosomes are present, thus establishing a dimorphism of the spermatozoa in both cases. Where different numbers separated by a hyphen are given under either the diploid or haploid columns, a number varying between the two has been found.

Group, Genus, Species.	Chromosomes in Sex Cells.		Somatic Cell.	No. of Chromo- somes.	Authority.
	Diploid No.	Haploid No.			
<b>VERTEBRATA</b>					
<b>MAMMALIA</b>					
<i>Homo</i> .....	♂ 22	♂ 10, 12 <sup>1</sup> ♂ 10-12 ♂ 12 ♂ ca. 12 ♂ 16			Guyer ('10) Montgomery ('12) Duesberg ('06) Jordan ('14) Moore and Arnold ('06)
			Cornea of eye	24	Flemming ('98)
			Mucus cells	32	Farmer, Moore, Walker ('05)
			Connective tissue	32	Farmer, Moore, Walker ('05)
			Lymph bodies	32	Farmer, Moore, Walker ('05)
			Liver	34	Wieman ('13)
			Brain	33, 34	"
			Mesenchyme	34, 38	"
			Intestinal meso- thelium	34	"
			Nasal epithelium	34, 38	"
	♂ 47 ♀ ca. 48	♂ 23, 24			Winiwarter ('12)
<i>Lepus cuniculus</i> ..	♂ ca. 22	♂ 11, 11 ♀ 10-12 <sup>2</sup>			Bachhuber ('16) Honoré
	♂ 28-36 ♀ 42		Epithelium of ear	28-32	Barratt ('07)
			Great omentum	42, 80	Winiwarter ('00)
			Amnion	42	"
			(not stated)	24	Flemming ('98) Stevens ('11b)
<i>Cavia cobaya</i> ....	♂ 56	♂ 28, 28			Flemming ('98) Stevens ('11b)
<i>Canis familiaris</i> ..			Mesoderm	etwa 24	Flemming ('98)
			Leucocyte	8	vom Rath ('94)
			Epithelium of bladder	8	" "
			Epithelium of bladder	32	" "
			Epithelium of bladder	64	" "
<i>Felis domestica</i> ...	♀ 36	♀ 12	(not stated)	36	Winiwarter and Sainmont ('09)
<i>Sus scrofa domes- tica</i> .....	♂ 18 ♀ 20	♂ 8, 10	♂ mesonephros	18	Wodsedalek ('13)
			♀ "	20	"
<i>Didelphys virgin- iana</i> .....	♂ 17	♂ 8, 9	Interstitial cell	17	Jordan ('11)
<b>AMPHIBIA</b>					
<i>Salamandra macu- losa</i> .....	♂ 24	♂ 12			Meves ('97)
			Pronephros.....	12	vom Rath ('94)
			Yolk	12	" "

<sup>1</sup> Guyer reports a further reduction in the second division to 5 and 7. This is accomplished by a fusion of the autosomes.

<sup>2</sup> Fide Winiwarter ('00).



Group, Genus, Species.	Chromosomes in Sex Cells.		Somatic Cell.	No. of Chromo- somes.	Authority.
	Diploid No.	Haploid No.			
<i>Salamandra macu- losa</i> .....	♂ 24	♂ 12	Blood Peritoneal endo- thelium Epithelium Connective tissue	12 19-27 24 24	vom Rath ('94) Della Valle ('09) Rabl ('06) <sup>1</sup> " Meves ('11)
<i>Amblystoma</i> .....		♀ 8 ♀ 15	Epithelium of gill 1st cleavage 1st " Cleavage Nerve Ectoplasm Muscle..... Pigment Connective tissue	24 16 ca. 30 12 24 24 24 24 24	Meves ('11) Fick ('93) Jenkinson ('04) Kölliker ('89) <sup>2</sup> Mack ('14) " " "
DIPNOI					
<i>Lepidosiren para- doxa</i> .....	♂ 38	♂ 19	Larval nerve Mesenchyme Ectoderm Chorda dorsalis Red blood cell	38 ca. 36 ca. 36 ca. 36 ca. 36	Agar ('11) " ('12) Murray ('06) " "
MOLLUSCA					
GASTEROPODA					
<i>Paludina vivipara</i> .	♀ 14	♀ 7	Cleavage Tissue cells	14 14	Popoff ('07) "
INSECTA					
DIPTERA					
<i>Drosophila amæna</i>	♂ 8		Larval, pupal and adult	8	Metz ('14)
	♀ 8				
<i>Drosophila quin- aria</i> .....	♀ 8		Larval, pupal, and adult	8	Metz ('14)
<i>Drosophila repleta</i>	♂ 12		Larval, pupal, and adult	12	" ('16) " ('14)
	♀ 12				
<i>Drosophila fune- bris</i> .....	♀ 10		Larval, pupal, and adult	10	"
<i>Drosophila tri- punctata</i> .....	♀ 8		Larval, pupal, and adult	8	"
<i>Drosophila ampel- ophila</i> .....	♀ 8		Larval, pupal, and adult	8	"
	♂ 8	♂ 4, 4	Segmentation Ovarian follicle	8 8	Stevens ('08a) "

<sup>1</sup> Fide Meves ('11).<sup>2</sup> Fide Jenkinson ('04).

Group, Genus, Species.	Chromosomes in Sex Cells.		Somatic Cell.	No. of Chromo- somes.	Authority.
	Diploid No.	Haploid No.			
<i>Eristalis tenax</i> ....	♂ 12	♂ 6, 6	Follicle of testis	12	Stevens ('08a)
			Ovarian follicle	12	"
<i>Calliphora erythro-</i> <i>cephala</i> .....		♂ 6	Somatic	12	Metz ('16)
	♀ 12				"
<i>Sarcophaga sarra-</i> <i>cinæ</i> .....	♂ 12	♂ 6			Stevens ('08a)
	♀ 12		Ovarian follicle	12	"
<i>Sarcophaga</i> sp....			" "	12	Metz ('16)
			Somatic	12	"
			"	24	"
			"	48	"
<i>Ravinia peniculata</i>	♀ 12		Ovarian follicle	12	"
<i>Homalomya</i> sp....		♂ 6	Somatic	12	Metz ('16)
<i>Fucellia marina</i> ..			Somatic	12	"
			"	24	"
			"	48	"
<i>Spogostylum sim-</i> <i>son</i> .....			Ovarian follicle	12	"
<i>Culex pipiens</i> ....	♂ 3	♂ 3	Undifferentiated		
			larva	3	Taylor ('14)
			Muscle	3	"
			Nerve	3	"
			♂ tracheal tube	3	"
			♂ Malpighian		
			tube	3	"
			♀ alimentary		
			canal	3	"
			♀ body wall	3	"
			♀ Malpighian		
			tube	3	"
			Egg follicle	3	"
		♂ 3			Stevens ('11a)
	♂ 6				"
	♀ 6				Metz ('16)
					Stevens ('11a)
					Metz ('16)
HYMENOPTERA					
<i>Apis mellifica</i> ....	♂ 16				Meves ('07)
		♂ 16			"
	♀ 16	♀ 8	Cleavage	32	Nachtsheim ('13)
			Blastoderm	32	Nachtsheim ('13)
			"	64	Petrunkewitsch ('01)
<i>Nematus ribesii</i> ..	♂ 8	♂ 4	Developing egg	8	Doncaster ('07)
	♀ 8	♀ 4	Ovary sheath	ca. 16	"
LEPIDOPTERA					
<i>Phragmatobia ful-</i> <i>ginosa</i> .....		♀ 28, 29	♀ blastoderm	58	Seiler ('14)
			♀ "	61	"

Group, Genus, Species.	Chromosomes in Sex Cells.		Somatic Cell.	No. of Chromo- somes.	Authority.
	Diploid No.	Haploid No.			
<i>Phragmatobia ful- ginosa</i> . . . . .	♂ 56	♂ 28	♂ blastoderm ♂ "	56 62	Seiler ('14) "
<i>Lymantria japon- ica</i> . . . . .		♂ 31 ♀ 31	Blastoderm	62	"
<i>Lymantria dispar</i> .		♂ 31 ♀ 31	Blastoderm	62	"
<i>Philosamia cynthia</i>	♂ 26	♂ 13 ♀ 13	Blastoderm	26	Dederer ('07) " ('15)
COLEOPTERA					
<i>Tenebrio molitor</i> .	♂ 20 ♀ 20	♂ 10, 10	♂ pupa Follicle of egg	20 20	Stevens ('05) "
<i>Elatér "I"</i> . . . . .	♂ 19		Follicle of egg	20	" ('06)
<i>Chelymorpha argus</i>	♂ 22	♂ 11, 11	Follicle of egg	22	"
<i>Odontota dorsalis</i> .	♂ 16	♂ 8, 8	Wall of testis	16	Stevens ('06)
<i>Trirhabda virgata</i> .	♂ 28	♀ 14, 14	♂ pupa Egg follicle	28 28	" "
<i>Trirhabda cana- dense</i> . . . . .	♂ 30	♂ 15, 15	Egg follicle	30	"
<i>Diabrotica vittata</i> .	♂ 21	♂ 10, 11 ♀ 11	Ectoderm " Neuroblast	22 21 21	" ('08b) Hoy ('14) "
<i>Photinus pennsylv- anicus</i> . . . . .	♂ 19 ♀ 20	♂ 9, 10	♂ digestive tract	19	Stevens ('09) "
<i>Photinus consan- guineus</i> . . . . .	♂ 19 ♀ 20	♂ 9, 10	Egg follicle	20	"
ORTHOPTERA					
<i>Gryllus domesticus</i>	♂ 21	♂ 10, 11	♂ somatic In larval ovary	20 20	Gutherz ('07) Baumgartner ( '04) Baumgartner ( '04) Gutherz ('07) "
<i>Leptophyes punc- tatissima</i> . . . . .	♂ 31 ♀ 32		Intestinal epithel- ium Oviduct	31 32	Mohr ('15) "
<i>Locusta viridissi- ma</i> . . . . .	♂ 29 ♀ 30		♂ somatic Oviduct	29 30	Mohr ('15) "
<i>Steiroxys trilineata</i>	♂ 29	♂ 14, 15	Epithelium of vas deferens	29	Davis ('08)
<i>Acridium granula- tus</i> . . . . .	♂ 13	♂ 6, 7	Epithelium of mesenteron Proctodeum Hypodermis Fat body Connective tissue	13 13 13 13 13	Robertson ('16) " " " "

Group, Genus, Species.	Chromosomes in Sex Cells.		Somatic Cell.	No. of Chromo- somes.	Authority.
	Diploid No.	Haploid No.			
<i>Acridium granulatus</i> .....	♂ 6, 7		Follicle of testis Giant cell-fat body Ovarian follicle	13 26 14	Robertson ('16) " "
<i>Acridium incurvatus</i> .....		♂ 6, 7	Follicle of testis	13	"
<i>Tettigidea parvipennis</i> .....	♂ 13 ♀ 14	♂ 6, 7	♂ fat body Ovarian follicle	13 14	" "
<i>Pamphagus mar-moratus</i> .....	♂ 19	♂ 9, 10	Ovarian follicle	20	Granata ('10)
<i>Aploplus mayeri</i> ..	♂ 35	♂ 17, 18	Egg follicle	36	Jordan ('08)
<i>Leucophæa maderiæ</i> .....	♂ 23 ♀ 24	♂ 11, 12	Follicle of ovary	24	Morse ('09) "
<i>Periplaneta americana</i> .....	♂ 32  ♂ 33 ♀ 34	♂ 16  ♂ 16, 17	Body tissues  Ovarian follicle	32  34	Farmer and Moore ('05) Morse ('09) "
<i>Blatta germanica</i> ..	♂ 23 ♀ 24	♂ 11, 12	Egg follicle	24	Wassilief ('07) "
<i>Anisolabis maritima</i> .....	♂ 24 ♀ 24	♂ 12, 12	Egg follicle	24	Randolph ('08) "
HEMIPTERA					
<i>Philænus spumaria</i> .....	♂ 23 ♀ 24	♂ 11, 12	Follicle ♀ somatic	23 24	Boring ('13) "
<i>Aphrophora quadrangularis</i> .....	♂ 23	♂ 11, 12	♂ larva	23	Stevens ('06)
<i>Pæcilopectera septentrionalis</i> .....	♂ 27	♂ 13, 14	♀ somatic	28	Boring ('07)
<i>Pæcilopectera pruinosa</i> .....	♂ 27	♂ 13, 14	Egg follicle	28	"
<i>Galgulus oculatus</i>	♂ 35 ♀ 38	♂ 16, 19	Ovarian follicle	38	Payne ('08) "
<i>Diplocodus exsanguis</i> .....		♂ 13, 13	♂ somatic ♀ somatic	26 26	Payne ('09) "
<i>Fitchia spinosula</i>	♂ 27	♂ 13, 14	♀ somatic	28	"
<i>Prionidus cristatus</i>	♂ 26	♂ 12, 14	♀ somatic	28	"
<i>Sinea diadema</i> ....	♂ 28	♂ 13, 15	♀ somatic	30	Payne ('09)
<i>Acholla multispinosa</i> .....	♂ 26 ♀ 30	♂ 11, 15	♀ somatic	30	" ('10) "
<i>Pyrrhocoris apterus</i> .....	♀ 24	♀ 12	Connective tissue Body cells' .....	24 24	Henking ('92) "
			Ovarian follicle	24	Gross ('07) Wil- son ('09c)
<i>Protenor belfragei</i> ..	♂ 23 ♂ 13 ♀ 14	♂ 11, 12 ♂ 6, 7			Wilson ('09a) " ('06) "
					Morrill ('10)

Group, Genus, Species.	Chromosomes in Sex Cells.		Somatic Cell.	No. of Chromo- somes.	Authority.
	Diploid No.	Haploid No.			
<i>Protenor belfragei</i> .		♀ 7	Cleavage	14	Morrill ('10)
			"	14	"
			Ovarian follicle	14	Wilson ('06)
<i>Syromastes mar- ginatus</i> .....	♂ 22	♂ 10, 12	Ovarian cells	24	Wilson ('09c)
<i>Anasa tristis</i> .....	♂ 21	♂ 10, 11			Wilson ('06)
	♀ 22	♀ 11			Morrill ('10)
					Wilson ('06)
			Cleavage	21	Morrill ('10)
			"		Hoy
				22	Morrill ('10)
					Hoy
			Ectoderm	21	Hoy Wilson ('06)
			"	22	"
			Mesoderm	21	"
			"	22	"
			Hypodermis	21	"
			"	22	"
			Neuroblast	21	Hoy
			"	22	"
			Ovarian follicle	22	Wilson ('06)
			Investing cell of ovary	44	"
<i>Archimerus alter- natus</i> .....	♂ 15		Cleavage	15	Morrill ('10)
	♀ 16	♀ 8	"	16	"
<i>Chelinidea vittigera</i>			Cleavage	21	"
			"	22	"
<i>Alydus pilosulus</i> ..	♂ 13	♂ 6, 7	Investing cell of testis	13	Wilson ('06)
	♀ 14		Egg follicle	14	"
<i>Metapodius ter- minalis</i> .....	♂ 21-26	♂ 11-16	Ovarian cells	22-25	" ('09b)
<i>Metapodius femor- atus</i> .....	♂ 22-28	♂ 12-16	" "	23-28	"
<i>Metapodius granu- losus</i> .....	♂ 22-27	♂ 12-17	" "	25-26	"
<i>Podisus spinosus</i> .	♂ 16	♂ 8, 8			" ('05a)
			♀ follicle cell		" ('06)
<i>Euschistus crassus</i>	♂ 12		♂ embryo	12	Foot and Strobell ( '12)
	♀ 12		♀ "	12	Foot and Strobell ( '12)
<i>Cænus delius</i> .....	♂ 14		♀ Follicle cell	14	Wilson ('06)
ODONATA					
<i>Anax junius</i> .....	♂ 27	♂ 13, 14	Follicle of ovary	28	Lefevre and Mc- Gill ('08)
Prototracheata					
<i>Peripatus balfouri</i>	♂ 28	♂ 14	Yolk cell of testis sheath	19	Montgomery ( '00)
	♀ 28		Blood cell	ca. 26	Montgomery ( '00)
			Endoderm	28	Montgomery ( '00)

Group, Genus, Species.	Chromosomes in Sex Cells.		Somatic Cell.	No. of Chromo- somes.	Authority.
	Diploid No.	Haploid No.			
<i>Peripatus balfouri</i>			Ectoderm	28	Montgomery ('00)
			Ovarian stalk cell	34	Montgomery ('00)
Crustacea					
<i>Branchipus grubei</i>	♀ 24	♂ 12 ♀ 12	Cleavage	24	Fries ('09)
			Intestinal epithelium	24	"
<i>Diaptomus cæruleus</i> .....	♂ 28 ♀ 28		Intestinal epithelium	14-28	Krimmel ('10)
			Nerve cells	14-20	"
			Muscle	14-28	"
			Hypodermis	14-20	"
Annelida					
<i>Phascolosoma vulgare</i> .....		♂ 10 ♀ 10	Late cleavage	10	Gerould ('06)
			Ectoderm of gastrula	10	"
<i>Ophryotrocha puerilis</i> .....	♂ 4 ♀ 4		Ectoderm	4	Korschelt ('95)
			Mesoderm	4	"
			Endoderm	4	"
			Blastula	4-8	"
	♂ 8	♂ 4	Somatic	8	Grégoire and De-ton ('06)
Nematoda					
<i>Stongylus paradoxus</i> .....	♂ 11 ♀ 12	♂ 5, 6 ♀ 6	Ectoderm	11	Gulick ('11)
			Endoderm	11	"
			Endoderm	12	"
<i>Angiostomum nigrovenosum</i> ....	♂ 11 ♀ 12	♂ 5, 6 ♀ 6	♂ 1st and 2nd cleavage	11	Schleip ('11)
			♂ blastula	22	"
			♀ 1st and 2nd cleavage	12	"
			♀ late embryonic stage	24	"
<i>Ancyracanthus cystidicola</i> ....	♂ 11 ♀ 12	♂ 5, 6 ♀ 6	Cleavage	11	Mulsow ('12)
			"	12	"
<i>Ascaris megalocephala (univalens)</i> .....	♂ 2 ♀ 2	♂ 1 ♀ 1	Cleavage	ca. 60	Brauer ('93) Boveri ('87) ('99)
Turbellaria					
<i>Planaria simplicissima</i> .....		♂ 3-4 ♀ 3-6	Somatic cell	6	Stevens ('04)
					"
Trematoda					
<i>Zögonus mirus</i> ...		♂ 5	Cleavage	10	Goldschmidt ('05)
	♀ 10	♀ 5	Tissue cells	10	Goldschmidt ('05)

Group, Genus, Species.	Chromosomes in Sex Cells.		Somatic Cell.	No. of Chromo- somes.	Authority.
	Diploid No.	Haploid No.			
<i>Zoögonus mirus</i> ...	♀ 10	♀ 5	Epithelium of vas deferens	10	Goldschmidt ( '08)
			Parenchyme	10	Goldschmidt ( '08)
			Epithelium of bladder	10	Goldschmidt ( '08)
	♀ 12	♀ 6	Interstitial Embryonic	12	Wasserman ( '13)
	♂ 12	♂ 6	Cleavage	12-14	"
		♀ 6	Ectoderm	12	Grégoire ( '09)
Hydrozoa				ca. 12	"
<i>Gonionemus mur-</i>					
<i>bachii</i> .....	♂ ca. 24	♂ 12	Cleavage	24	Bigelow ( '07)
	♀ ca. 24		Endoderm	24	"

The chromosome number appears to vary in a variety of forms. Many reports are apparently antagonistic. It may be that in certain animals the chromosome number differs in different individuals. Evidently much fruitful work can be done in attempting a solution of such differences.

The chromosome counts in man are difficult of explanation due to the diverse and conflicting results obtained in studies of spermatogenesis. On the face of the evidence it would almost appear that the chromosome number varies. Since Guyer and Montgomery, as well as Jordan, worked on negroes and their results approximate, and since Winiwarter obtained his results from a white man, it has been suggested (Guyer, '14, and Morgan, '14) that the number of chromosomes differs in the two races. If this is true, hybrids might show an intermediate number of chromosomes. Wieman's results, however, contradict this, unless there is a synpasis of some of the chromosomes in somatic cells. Outside of Flemming's count of 24, the counts in somatic tissues show a number of chromosomes varying between 32 and 38. Moore and Arnold report a haploid number of 16. This approaches most nearly to these numbers in the somatic cells. Jordan does not hold to the exact haploid number of 12, for though the number is not lower in his preparations, he states that it may be higher by several more chromosomes. Wilcox

('00) reports a number varying between 15 and 19, though he considers 18 as the normal number. However, he does not state if this number is the haploid or diploid; the inference is that it is the former. The counts of somatic chromosomes reported by Farmer, Moore and Walker were made from cells in a normal rectum in comparison with cancerous tissue. Wieman worked on a white human embryo. He points out the fact that the number is at variance with that reported by most investigators as the diploid number of the sex cells, and suggests that the varying counts which he made in the soma were due to a breaking up of some of the larger chromosomes. The difference between the somatic and spermatogonial numbers may be due, he thinks, to a similar process. Wieman also suggests that a doubling of the chromosomes may have taken place in Winiwarter's material. Precocious division of some of the chromosomes may also give this result.

In the somatic cells of the rabbit Winiwarter obtained a chromosome number varying between 40 and 80. The majority of counts showed 42, and this he considers the normal number. This number corresponds to the number of chromosomes in the oögonia, but a haploid number of 10-12 in the maturation divisions of the egg was reported by Honoré, one of Winiwarter's students. This latter count closely approximates the observations of Bachhuber on the number of chromosomes in the spermatogonia. Winiwarter draws an analogy to the case of *Ascaris*. However, the analogy will only hold if the "oögonium" was in reality a follicle cell or some other non-germinal cell, otherwise it would seem to be analogous to the double reduction reported by Guyer in man and the domestic fowl. Apparently the cell in question was not an oögonium. Flemming modifies his number of 24 chromosomes by the statement that the number may be even higher. Barratt's numbers are intermediate between the two extremes. With reference to the varying number of chromosomes which he reports, he suggests that such variation may be entirely normal and occur regularly.

Flemming quotes Bardeleben's count of 16 chromosomes in the spermatogonia of the guinea pig, but fails to find a number corresponding to this in a study of an embryo. His number of



24 is only approximate. Taking Miss Stevens's results as a standard this number would seem to indicate a number of chromosomes in somatic cells corresponding to the haploid number in the germ cells.

Vom Rath's observations on the dog were made on a three weeks' old animal. He qualifies his remarks with the statement that owing to the small size of the chromosomes he was able to make only an approximate enumeration. In addition to the variations in the blood cells and the bladder he found great variation in the spleen, the bone marrow and in the testis. He considers 32 as the typical number, and points out that this number, together with the variations, is a multiple of eight, which number he also found, thus showing that the chromosomes may be bivalent, quadrivalent, or even polyvalent. The fact that he frequently found multipolar mitoses seems to indicate that his material may have been abnormal.

The observations of Winiwarter and Sainmont on the cat are comparable to those of the former on the rabbit. The probability here is that there is a breaking up of the chromosomes in the somatic cells.

Vom Rath considers the chromosomes in the somatic tissues of *Salamandra* as bivalent. However, his statement "hatte ich . . . mit absoluter Sicherheit nur 12 Schleifen (Aequator 24) gefunden" is not clear. Rabl and Meves conclude that chromosome pairs cannot be distinguished in the somatic cells. Della Valle, as a result of finding a chromosome number of between 19 and 27, considers the number variable and the chromosomes as temporary and variable organizations of chromatin, which appear in the prophase and dissolve in the telophase. The number of the chromosomes is simply the quotient of the quantity of the chromatin.

Mack states that the number of chromosomes in the somatic cells of *Amblystoma* agrees with the number in the primary spermatocytes. Jenkinson merely states that his observations are not in accord with those of Fick and Kölliker.

With reference to Murray's count of 36 chromosomes in *Lepidosiren* Agar says (p. 5): "Murray gave the somatic number as probably thirty-six, which is as near the right number as could

be expected to be arrived at from the somatic mitoses with their long chromosomes."

In the Diptera Metz has reported that the somatic chromosomes are closely paired together. In the case of *Sarcophaga* and *Fucellia* the groups of 24 and 48 chromosomes represent multiple groups, and the arrangement of the chromosomes is in tetrads rather than in pairs.

In her paper on *Culex pipiens* Miss Taylor takes up in detail the work of Miss Stevens on *Culex pungens*, and is evidently unaware of the fact that Miss Stevens published a paper on *pipiens* a few years later. Miss Taylor considers the presence of six chromosomes in Miss Stevens's material as due to a precocious splitting or division of the diploid number of three. Miss Stevens described a parasynapsis or side-by-side union of the chromosomes in each cell generation. This Miss Taylor thinks may offer a clue to the conditions she found in *pipiens*, namely that in this species "parasyndesis" is converted "into actual fusion, thus resulting in the formation of three out of six chromosomes." She offers as an alternative the suggestion that one of the pronuclei does not take part in development. Her results are not entirely convincing, especially since she found stages in many of the somatic cells comparable to synizesis stages in spermatogenesis. This seems to show that perhaps her material was not of the best. Metz has found that the method of securing the preparations of the testes employed by Miss Taylor, namely that of fixing either the whole or a large part of the insect entire, results in a "clumping or running together of the chromosomes, which is exactly the kind of behavior that would cause pairs to give the appearance of single chromosomes" (p. 226). He agrees with Miss Stevens's observations.

In the spermatogenesis of the bee, according to Meves, there is no reduction division. Nachtsheim considers 32 as the normal number. The 16 chromosomes in the oögonia are bivalent, likewise the 8 which form the haploid number. Similarly a haploid number of 8 chromosomes has been reported in the spermatocytes, which is due to this "Chromosomenkoppelung." Here these also would be bivalent. Though the reports of several investigators tend to show that the number of chromo-

somes varies in the bee, the number is always eight or a multiple of this. This agrees with Petrunkevitch's theory that the 64 chromosomes, which he found in cells of the blastoderm of fertilized eggs, were due to a splitting up of quadrivalent chromosomes. A similar fragmentation appears to be characteristic of parthenogenetic individuals, *i. e.*, the drones. This is also the case in other Hymenoptera, as Armbruster reported in *Osmia*, and Granata in *Xylocopa*.<sup>1</sup>

In *Nematus* Doncaster suggests that perhaps the chromosomes of the germ cells "may be compound and consist of a number of smaller units which become separated in somatic cells" (p. 107).

The case of *Phragmatobia* is interesting since in this form Seiler has demonstrated a dimorphism of the eggs with respect to their chromosome content. The female diploid complex is composed of an  $x$ , 2  $y$ 's, and 54 autosomes. The counts made in the blastoderm of developing eggs can be analyzed as follows: The 58 complex is due to a splitting in two of the large  $y$ -chromosome, and is from a female. The complex with 61 chromosomes is also from a female in which the  $x$ -chromosome has split up into four segments and the large  $y$ -chromosome has also split up into two parts. The complex with 62 chromosomes is from a male where the two  $x$ -chromosomes have each split up into four segments. "This striking explanation has absolutely nothing improbable about it, since a splitting of the sex chromosomes in the somatic nuclei has been observed quite often" (trans).

In *Gryllus domesticus* Gutherz found that the accessory chromosome is absent in the cells of the soma. This can be explained, he says, only by assuming a "Diminutionsprozess" or by assuming that since the accessory chromosome does not participate in the early stages of development, it does not make its appearance until later. Either of these explanations, he thinks, places the theory of the individuality of the chromosomes in an extremely delicate position.

Robertson considers that the cells in *Acridium* containing 26 chromosomes are double cells with double sets of cell organs. These may have been produced by the fusion of two cells or by the suppression of cell division after nuclear division had taken place.

<sup>1</sup> Fide Buchner (Referate), Arch. f. Zellf., Bd. 5, H. 3 (1910).

Farmer and Moore do not hold strictly to the number of 32 chromosomes in the cells of the cockroach. Cells were found which differed by one or several chromosomes.

Variation in the number of chromosomes in *Metapodius* affects only one class of chromosomes, the "supernumeraries." Wilson considers the 22-chromosome type as the typical. This type possesses an unequal pair of idiochromosomes. The 21-chromosome type is derived by the disappearance of the small idiochromosome. The numbers above 22 are due to the presence of one to six supernumeraries. This variation of the chromosome number is chiefly between different individuals, for owing to the irregular distribution of these supernumeraries in the maturation divisions of the sperm cells, the number each sperm receives is variable. Further variations may occur in individual cells.

The count of 19 in *Peripatus* may be due, according to Montgomery, to the fact that not all of the chromosomes were contained in one section. This may also answer for the count of 26. The count of 34 was made from two sections, and he suggests that it is possible that parts of some chromosomes were in both sections. In this way some of the chromosomes were counted twice.

Krimmel finds that in the somatic tissues of *Diaptomus* the number of the chromosomes varies between the reduced and the diploid number. This is brought about by fusion of some or of all of the chromosomes into tetrads, or the chromosomes may appear bi-partite. "Man wird hier wie bei den generativen Zellen daran denken dürfen, dass in diesen Fällen die Einknickung oder scheinbare Querkerbe der in der Reifungsperiode auftretenden Querkerbe entspricht, dass also das Zeichen der synthetischen Aneinanderfügung zweier Chromosomen noch nicht verschwunden wäre" (Krimmel, '10, p. 790).

Gerould says: "In *Phascolosoma vulgare* I have uniformly found 10 chromosomes in the late cleavage and in the gastrula . . . each of which I regard as bivalent" (footnote, p. 87).

In addition to the cells containing four chromosomes in *Ophryotrocha*, Korschelt found eight chromosomes in some of the cells of the blastula. He believes that this number is due to a transverse splitting of the four chromosomes. Grégoire and

Deton, however, claim that eight and not four is the normal and characteristic number.

In *Angiostomum* the chromosomes fragment in the cells of the soma. The chromosomes of the sex cells are apparently bivalent.

The chromosomes of the somatic cells in *Ascaris* are derived from a fragmentation of the compound chromosomes of the sex cells. This fragmentation is accompanied by a "chromatin diminution."

Miss Stevens concluded in the case of *Planaria* that two interbreeding forms were present. The pairing of two individuals with different chromosome numbers would explain, she writes, the varying chromosome numbers she obtained.

Wasserman and Grégoire have disputed the counts of Goldschmidt in *Zoëgonus*. It may be that two different varieties have been concerned, one with a chromosome complex of 10, and the other with one of 12 or more.

In considering the foregoing cases it is apparent that in general the behavior of the chromosomes in the somatic cells can be classified in the manner stated in the introduction to this paper, namely that (1) the somatic and gonial chromosomes agree in number and type, (2) the number of the chromosomes in the somatic cells is higher than in the germ cells, due to a splitting or fragmentation, (3) multiple chromosome groups are produced by the suppression of a cell division, and (4) there is a synapsis, more or less permanent, of all or certain pairs of chromosomes in each cell generation. It is also evident that there are numerous cases which are exceedingly perplexing, and which cannot be classified at the present time.

The majority of animals, particularly the insects, in which group more work of a cytological nature has been done than perhaps in any other, can be included in the first category. But even here the classification is not sharp and distinct for many forms may show at the same time the third type of chromosome behavior in one or several tissues. This, however, does not seriously affect the main conclusion, and is possibly to be considered as no more than a normal variation.

When a sufficiently detailed study shall have been made of the somatic chromosomes where some or all of these are represented

in the germ cells by compound chromosomes, it is highly probable that the number of the chromosomes will be found to be the same in all of the somatic tissues. In this type of somatic chromosome behavior we find two distinct cases, one where, as in *Phragmatobia*, there is only a splitting up of one or at the most a few chromosomes, and the other where all of the chromosomes in the germ cells are apparently compound, and each breaks up into its component parts in the somatic cells (Hymenoptera, Nematoda, and perhaps some of the vertebrates).

The synopsis of homologous pairs of chromosomes in somatic cells was described by Miss Stevens ('08, '10) in the case of a number of species of the Diptera. This synopsis apparently took place in the anaphase or telophase and lasted until the metaphase of the next division. Metz ('14, p. 55-56) confirms this: "The *Drosophilas* offer some of the most striking evidences of the actual pairing of chromosomes in the diploid groups, thus far observed. The phenomenon is apparently characteristic of all Diptera, but is nowhere so striking as in this genus. . . . But the most remarkable feature of the whole study is the discovery that the chromosomes not only exhibit a close association in pairs at nearly all times, but that before every cell division the members of each pair become so intimately united that they may be said actually to conjugate. Each pair, with the possible exception of the sex-chromosomes, goes through what amounts to a synopsis in every cell generation, so that in many cases the figures closely resemble those of the haploid groups. Apparently this takes place in every prophase, but a second conjugation may occur during metaphase, just a short time before division." This latter statement he qualifies in his later paper saying that it is "of only occasional occurrence and is not a uniform stage in chromosomal activities" ('16, p. 230). In this paper he presents the results of his study of this chromosome pairing in about 80 species of Diptera, where he has found it to be of uniform occurrence throughout the developmental history of the individual. He concludes that this paired arrangement is "selective to the highest degree," that the members of the pair represent, one a maternal and one a paternal chromosome, and that this pairing shows that the chromosomes (forming a pair) are qualitatively,

i. e., physico-chemically, similar. This latter idea is further developed, and he thinks that this assorting of the chromosomes in pairs demonstrates a qualitative difference of the *pairs*.

The view that the chromosomes may be the same in number and type in all the cells of the body, or that fragmentation or transverse splitting on the one hand, and fusion of pairs on the other hand may account for differences is challenged by a number of investigators, who believe that a limited degree of variation may really occur (Barratt, Gutherz, Farmer and Moore, Della Valle, Rabl, Meves, Foot and Strobell). If there may be variation in the number of the chromosomes in various cells of the same individual, it is certainly not of general occurrence, and no really clear case has been presented. I believe that variation in number is more often between individuals of the same species than between cells or tissues of the same animal. Variations in the size of chromosomes are more difficult of analysis, and more difficult of demonstration. In *Anasa* it is clear that the chromosomes of any cell maintain the typical size relations, so that particular pairs can be picked out with little trouble. The results of Rabl and Meves are the reverse of this. Foot and Strobell ('13) write: "We demonstrated in 1905 that the form and relative size of the chromosomes in *Allolobophora fatida* are inconstant and in every publication since that date we have demonstrated variability in form, relative size and behavior of the chromosomes in every form we have studied, and we have consistently argued that such variability attacks the very foundations upon which the popular chromosome speculations of this decade have been built."

Before many of these questions can be satisfactorily answered detailed study must be made of the chromosomes in the somatic cells of many more forms, especially where the somatic and gonial numbers do not agree. Also a thorough review must be made of the many apparently aberrant cases, which have been briefly considered here.

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